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LOSSES OF NATIVE PLANT SPECIES FROM WORCESTER, MASSACHUSETTS

ROBERT I. BERTIN

Biology Department, Holy Cross College, Worcester, MA 01610
e-mail: rbertin@holycross.edu

ABSTRACT. I recorded the extant vascular flora of Worcester, Massachusetts in seven years of field work beginning in 1994 and obtained historical records from herbarium specimens and the published literature. A detailed vascular flora of the City was published elsewhere. This paper updates the flora with information from an important and previously overlooked collection of specimens, and examines the apparent historic losses of native species in relation to habitat and taxonomy. Overall species losses were about 18% in the past century. Losses were particularly high among species associated with aquatic habitats, bogs, and calcareous or circumneutral terrestrial habitats. I suggest that the first of these reflects extensive alteration of many bodies of water through siltation, chemical pollution, eutrophication, and stream channelization. Losses in the remaining two habitat types may reflect the initial rarity of such habitats within the City combined with habitat destruction. Losses were especially high in several families, including the Orchidaceae, Ophioglossaceae, Caryophyllaceae, Menyanthaceae, Lentibulariaceae, and Lamiaceae. High losses of aquatic and bog species have been noted in other areas, and high losses among orchids appear to be nearly universal. A combination of changing land use, habitat fragmentation, successional changes, species introductions, and climate changes are likely to cause further species losses in the decades ahead.

Key Words: species loss, biodiversity, habitat destruction, Worcester, orchids, flora

Despite the common knowledge that many human activities decrease biological diversity, such changes are only occasionally documented in the literature, and even less commonly subjected to any formal analysis. Documentation and analysis of species losses are, however, critical to efforts to manage for biological diversity and to minimize future species losses.

Vascular plants are probably one of the groups most suited to the evaluation of species losses. In temperate areas, at least, they are relatively well studied. In the eastern United States, recensuses have taken advantage of published floristic records from the 1800s or early 1900s for a variety of study areas ranging from individual plots (Curtis 1959) and single nature preserves or areas of equivalent size (Deane 1896; Pease 1911), to towns, cities, and counties (Darlington 1853; Hollick and Britton 1879; Owen 1888).

Repeated censuses of particular areas can provide various data, including numbers of species lost and rate of species loss. Such data also permit evaluation of losses in relation to life history attributes, habitat type, and taxonomic affiliation. Many studies of species loss report overall losses, but attempt little further analysis. Notable exceptions include the evaluation of species losses in relation to ecological attributes on Staten Island (Robinson et al. 1994) and in Wisconsin (Wiegmann et al. 2001), in relation to habitat and taxonomy in Massachusetts (Drayton and Primack 1996), and in relation to habitat, growth form, and taxonomy in Singapore (Turner et al. 1994).

Evaluation of losses in areas differing in geography and size, and subjected to different intensities and kinds of disturbances are likely to be particularly valuable. We are currently ill-equipped to say how the characteristics of the lost flora differ at the levels of a nature preserve, a town, a county, and a state; how sensitive rates of species loss are to the size of the area sampled; and how different types of disturbances (e.g., urbanization, agriculture, recreational use) influence the kinds of species lost. Only after analysis of a variety of sites will we be able to answer these questions. The present study is one step in this direction. It examines changes in the vascular flora of Worcester, Massachusetts, one of the largest New England cities, over a period of approximately 100 years. I focused especially on species losses in regard to taxonomy and habitat affiliation.

MATERIALS AND METHODS

Description of the study area. The City of Worcester lies in south-central Worcester County, Massachusetts, covering an area of 9740 ha. It falls largely within the drainage of the Blackstone River, which flows to Narragansett Bay, though a small area of northern Worcester is in the drainage of the Nashua and Merrimack Rivers. The City lies along an ill-defined north-south escarpment that separates lower land (~100 m elevation) to the east and south from higher land (~300 m) to the west and north. The bedrock consists largely of highly metamorphosed rocks of Silurian and Devonian age. The bedrock is covered by till in most areas, with smaller areas occupied by glacial outwash.

Perhaps 300 Indians occupied the area of Worcester prior to European colonization. Permanent European settlement began in the early 1700s, and a major increase in population occurred in the middle 1800s (Anonymous 1879). The original forested landscape gave way to agriculture, which then decreased over the past century. Intensive industrial, commercial, and residential development began in the 1800s and continues to the present. Today, Worcester consists of an urban core, with large buildings, extensive paved areas, and occasional landscaped grounds and vacant lots. Fingers of intensive development extend from the core along major roads towards the edges of the City. Surrounding the areas of intensive development are extensive residential neighborhoods, most of which contain scattered parks and undeveloped land. Closest to the City's perimeter, especially on the west side, are larger areas of undeveloped land, mostly forested.

Historical records of the flora. I used a combination of herbarium records and published reports to document the historical native flora of the City. One important collection is housed in Hadwen Herbarium at Clark University (CUW). Most of these specimens were collected between 1920 and 1955 by a group of botanists active in the Worcester region, including Mary Dodge, Burton Gates, W. H. Hodge, David Potter, George Pride, Norman P. Woodward, Burton N. Gates, and Winifred C. Gates. A second important collection includes specimens of the Worcester Natural History Society (unofficially abbreviated WNHS), housed at the Ecotarium in Worcester. These were collected in the late 1800s and early 1900s by a variety of collectors, including Norman P. Woodward, Katherine I. Fish, Mary C. Dodge, and G. E. Stone. These specimens were not cited in the Worcester flora (Bertin 2000) because I was unaware of their existence. New species from this collection are therefore documented in this publication. Additional records came from the Gray Herbarium (GH) and the herbarium of the New England Botanical Society (NEBC), including collections by Hattie Merrifield in 1879–1880 and K. M. Wiegand, collecting in 1911, and from the herbarium of the University of Massachusetts (MASS).

Supplementing the herbarium specimens were several published sources, including Jackson's (1909) *A Catalogue of the Flowering Plants and Ferns of Worcester County*, an addendum to this flora (Jackson 1927), Tucker's (1894) *Trees of Worcester*, Stone's (1899) *Flora of Lake Quinsigamond*, and lists of Potter and Woodward (1935) and Potter et al. (1940). The published sources and herbarium records do not represent a snapshot of one historical time, but rather record species present at some point in the late 1800s or early 1900s.

Records of the current flora. Intensive field work to inventory the current flora ran from 1994–1996, and less intensive work continued into 2001. I made several hundred separate visits to over 70 sites during this period. These sites included the range of natural and disturbed habitats found in the City. Records were kept of all native and introduced species, and herbarium specimens of approximately 70% of the extant flora were deposited at MASS.

Data analysis. In analyzing species loss by habitat, I used habitat descriptions reported in three published floras covering the study area. I used published information rather than my own assessments to prevent possible bias. I used data from more than one flora to allow for the variation in habitat designations in the different publications. The floras were Gleason and Cronquist (1991), Magee and Ahles (1999), and Seymour (1982). I created a spreadsheet data file including names of all native species that have been reported in Worcester and habitat descriptions supplied in each of the three references. I then established several habitat categories (Table 1), and identified a series of terms found in the floras that fitted each category. For example, bog habitat was designated by a single term: "bog." Rock outcrop habitat was designated by the terms: "cliff," "crevice," "ledge," "outcrop," and "rocks." The categories were chosen to represent a variety of habitats that could be distinguished using terms in the floras. Some categories overlap, and some species were present in more than one category. A computerized search permitted the listing of species in each habitat category in each literature source. For a few habitat categories it was then necessary to examine the species list and delete species clearly inappropriate to that category. For example, one search term for aquatic habitat was "stream." However, this term triggered inclusion of species such as spicebush [*Lindera benzoin* (L.) Blume], which was listed in one flora as occurring "along streams."

To determine habitats associated with particularly high losses,

Table 1. Habitat categories examined in this study, along with the habitat terms in floras that were used to assign species to these categories.

Habitat Category	Habitat Terms
Aquatic	Brooks, floating, lakes, pond, pool, rivers, springs, streams, submersed, water (excluding such combinations as "along rivers")
Bogs	Bog
Burned areas	Burn, fire
Calcareous terrestrial	Alkaline soil, basic soil, calcareous, circumneutral soil, limy soil, neutral, sweet soil (excluding aquatic species)
Coniferous	Cedar, conifer, pine, *Thuja*
Disturbed sites	Buildings, compacted soil, cultivated, disturb, dooryards, dumps, dwellings, garden, gravel pits, henyards, lawn, paths, pavement, railroad, roadside, sidewalks, stone walls, waste, weed
Dry herbaceous	Dry field, dry gravelly field, dry meadow, dry open place, dry sandy fields
Grasslands	Field, grass, meadow, pasture, prairies
Herbaceous	Field, grass, marsh, meadow, openings, pasture, prairies
Rich terrestrial	Fertile, rich
Rock outcrops	Cliff, crevice, ledge, outcrop, rock
Sandy substrate	Sand
Shrub swamps	Shrub swamp
Successional	Abandoned field, old field, seral, successional
Swamps	Swamp
Vegetated wetlands	Bog, marsh, miry, mucky, mud, peat, poorly drained sites, sedge mats, swamp, wet
Wet herbaceous	Low meadow, marsh, moist meadows, peaty meadow, springy meadow, swampy field, wet field, wet grassland, wet meadow, wet sunny
Woods	Forest, wood

the number of species lost in a particular habitat category was compared to the overall rate of species loss using exact probabilities based on a binomial distribution. For example, of 797 native species documented by either herbarium specimens or my sight records, 147 (18.4%) have disappeared. Gleason and Cronquist (1991) report 9 of the 797 native species as being associated with rock outcrops. Of these, two have disappeared in Worcester. Randomly sampling nine species from a universe in which 18.4% of species have been lost, one can use the binomial distribution to calculate the probability that 0, 1, 2, 3, 4, 5, 6, 7, 8, or 9 of the nine species will have been lost. By summing the last eight of these individual probabilities, one finds that the probability of losing two or more of nine randomly selected species is 0.52. Losses in a particular habitat were considered significantly different from the overall rate of loss if the likelihood of such a loss occurring by chance was less than 0.05. Because 0.52 exceeds 0.05, I conclude that Worcester's rock outcrop species have not been particularly prone to local extinction.

A similar approach was used to analyze species disappearances by plant family. Here the grouping was by plant family and the question asked was: "Given the overall rate of species loss, which families showed significantly different extinction rates than the flora as a whole?"

All species and family designations were based on Gleason and Cronquist (1991). The rates of loss reported in this paper are based on species documented by an herbarium specimen (the vast majority) or by my sight record (collectively referred to as documented species). I also performed a second set of analyses that included documented species plus those reported in the literature (total species). I report the results of significance tests involving this group of species, but not the data themselves, which paralleled the results for documented species.

Comparisons of species losses in Worcester to state-wide patterns of rarity were made using published data from the Massachusetts Natural Heritage Program (Sorrie and Somers 1999). The Massachusetts species at greatest risk are referred to herein as state-listed species, comprising species that are designated by the state as endangered, threatened, or of special concern. Species referred to herein as watch list species are those species given this informal designation by the Natural Heritage Program. These species are not formally listed, but flagged for monitoring. For each of these two groups (state-listed and watch list), I calculated the likelihood of obtaining as many listed species among the extirpated Worcester species if sampling randomly from the native species originally present in the City using exact binomial probabilities.

Changes in the extent of several habitats in the past two centuries were gauged by examining United States Geological Survey topographic maps drawn in 1935, 1951, 1971, and 1982, along with a hand-drawn map of the City from 1830. Only three habitats could be distinguished from the maps: forest, wetland, and water. I placed a grid of 5 mm squares on a transparency over each map, and recorded the number of grid points falling in each of the three habitats, along with the total number of grid squares within City boundaries. The total number of grid squares was at least 3300 for each map. The proportion of grid squares falling within each of the three habitats was taken as the proportion of that habitat in the City at that time.

RESULTS

The analyses presented herein are based on a total of 820 native species. Of these, 797 were documented species and the remaining 23 species were recorded only in published literature and were not observed by me. Most species on which my analyses are based are listed in Bertin (2000), and are not repeated here. However, examination of Worcester Natural History Society (WNHS) specimens at the Ecotarium and a few others yielded several dozen additions and changes, listed in the Appendix. Of the 820 total species, 170 (20.7%) are no longer found in Worcester. Of the 797 documented species, 147 (18.4%) no longer occur.

The extinction rates for most habitat categories did not deviate significantly from the overall extinction rate (Table 2). However, four habitats showed significantly greater than average extinction rates in at least one analysis. Species losses from bogs were significantly higher than average for both total losses and documented losses no matter which flora was used for habitat classification. Documented species losses from calcareous terrestrial habitats were significantly greater than average for two sources and for aquatic habitats and coniferous forest for one source each. Three habitats showed species losses that were significantly less than overall losses for one source: disturbed sites, herbaceous vegetation, and swamps.

In the taxonomic analysis, six families had documented local extinction rates significantly higher than for the overall flora: Menyanthaceae, Ophioglossaceae, Lentibulariaceae, Orchidaceae, Caryophyllaceae, and Lamiaceae (Table 3). All but the last family also show significantly elevated species losses when undocumented records are included.

The species lost from Worcester reflect at least partly the patterns of species decline in the entire state. This is illustrated by the fact that the proportions of state-listed and watch list species among those extirpated from Worcester are much greater than the

Table 2. Documented proportion of species lost by habitat category. Sample sizes in parentheses represent the presumed original species numbers in each habitat. Significant departures from the overall extinction rate are denoted as follows: * significantly greater, documented species; † significantly greater, total species; # significantly less, documented species; + significantly less, total species.

Habitat Category	Gleason & Cronquist	Magee & Ahles	Seymour
Aquatic	0.28 (79)*†	0.22 (77)†	0.25 (60)†
Bogs	0.35 (66)*†	0.33 (72)*†	0.39 (51)*†
Burned areas	0.25 (4)	1.00 (1)	1.00 (1)
Calcareous terrestrial	0.25 (20)	0.86 (7)*†	0.40 (15)*
Coniferous	0.50 (8)*†	0.23 (31)	1.00 (1)
Disturbed sites	0.16 (83)	0.11 (215)#+	0.13 (68)
Dry herbaceous	0.31 (16)	0.14 (43)	0.11 (35)
Dry open woods	0.09 (11)	0.29 (21)	0.11 (27)
Grasslands	0.18 (139)	0.15 (305)	0.20 (157)
Herbaceous	0.16 (171)	0.15 (337)#+	0.19 (167)
Rich terrestrial	0.24 (50)	0.19 (104)	0.15 (97)
Rock outcrops	0.22 (9)	0.21 (14)	0.20 (20)
Sandy substrate	0.19 (80)	0.25 (71)	0.17 (52)
Shrub swamps	– (0)	0.09 (23)	– (0)
Successional	0.05 (20)	0.15 (13)	– (0)
Swamps	0.20 (108)	0.13 (135)#	0.16 (144)
Vegetated wetlands	0.19 (275)	0.17 (285)	0.16 (268)
Wet herbaceous	0.11 (47)	0.17 (160)	0.12 (17)
Woods	0.18 (390)	0.17 (491)	0.16 (313)

proportion of the listed species among the extant flora (Table 4). For example, state-listed species comprise less than 1% of the extant native Worcester flora, but make up 9.5% of the extirpated native Worcester flora. Similarly, watch list species comprise 1.2% of the extant flora, but 12.2% of the extirpated flora. In each case, the proportion of listed species among the extirpated flora is significantly greater than among the group of all native species known to have existed in Worcester ($P < 0.001$, exact binomial probability).

The extent of forested, wetland and aquatic habitats changed in Worcester during the period 1830–1982 (Table 5). Forest habitat was low in the 1800s and early 1900s, increased during the middle 1900s, and decreased again in the late 1900s. Wetland habitat decreased substantially from the 1800s to the 1900s. Aquatic habitats increased from the 1800s into the early and mid 1900s and then decreased in the past 50 years.

Table 3. Proportions of species lost in families having lost more than a third of original species. Families with two or fewer species are excluded. Numbers of species per family are given in parentheses. * denotes significant departures from extinction rates in overall flora.

Family	Total Species Loss	Documented Species Loss
Menyanthaceae	1.00 (2)*	1.00 (2)*
Ophioglossaceae	0.83 (6)*	0.83 (6)*
Ulmaceae	0.67 (3)	0.67 (3)
Fumariaceae	0.67 (3)	0.67 (3)
Lentibulariaceae	0.67 (6)*	0.60 (5)*
Haloragaceae	0.60 (5)	0.50 (4)
Orchidaceae	0.57 (21)*	0.53 (19)*
Caryophyllaceae	0.56 (9)*	0.56 (9)*
Lamiaceae	0.40 (15)	0.40 (15)*
Onagraceae	0.40 (10)	0.40 (10)
Sparganiaceae	0.40 (5)	0.25 (4)
Potamogetonaceae	0.36 (14)	0.25 (12)

DISCUSSION

The overall species loss in Worcester is approximately 18% if one considers only species that have been documented with herbarium specimens and 21% if one additionally considers species listed for the City only in published records. Several sources of error are likely to influence these numbers. Despite the considerable amount of time that I spent in the field, my records are certainly incomplete, and populations of a few species listed here as extirpated probably remain in the City. Studies from other areas are replete with examples of species reappearing that were once thought to be locally extinct (Dickson et al. 2000; Kent 1975). An opposing source of error is the incompleteness of the earlier records. Most of the 64 previously unrecorded native species probably were present but overlooked in earlier work, though a few could be recent colonizations. Subtracting 64 species from the number of total known species (820) and documented species (797), leaves the actual numbers of historical records (756 and 733, respectively) from which the losses are derived. In percentage terms, the losses then represent 22.5% of total species and 20.0% of documented species. The presence of any undiscovered species with historical records would lower these numbers, but they are probably accurate within a few percentage points.

Table 4. Species loss and persistence among state-listed and watch list species. * species represented by specimens; † *Cypripedium calceolus* is represent by two varieties, recognized as species in Sorrie and Somers (1999), one endangered, one on the watch list; H = historical, E = endangered, T = threatened; SC = special concern. All species are native.

State-listed Species	Watch List Species
EXTANT	
**Arabis laevigata* (Muhl.) Poir.; T	*Asclepias tuberosa* L.
**Elymus villosus* Muhl.; T	**Bidens discoidea* (Torr. & A. Gray) Britton
**Potamogeton vaseyi* J. W. Robbins; E	**Eragrostis capillaris* (L.) Nees
	Isotria verticillata (Willd.) Raf.
	Juglans cinerea L.
	**Polygala verticillata* L.
	**Ribes americanum* Mill.
	**Sporobolus cryptandrus* (Torr.) A. Gray
Extant state-listed species = 3/650 = 0.5% of total and documented species	Extant watch list species = 8/650 = 1.2% of total and documented species
EXTIRPATED	
**Adlumia fungosa* (Aiton) Greene; T	**Bidens beckii* Torr.
**Arethusa bulbosa* L.; T	**Botrychium lanceolatum* (S. G. Gmel.) Ångstr.
**Asclepias purpurascens* L.; T	**Botrychium matricariaefolium* A. Braun
Castilleja coccinea (L.) Spreng.; H	**Botrychium oneidense* (Gilbert) House
**Cypripedium calceolus* L.; E†	**Cardamine rhomboidea* (Pers.) Alph. de Candolle
**Eriophorum gracile* W. D. J. Koch; T	*Carex diandra* Schrank
Galium boreale L.; E	*Carex haydenii* Dewey
**Habenaria flava* (L.) R. Br.; T	**Chenopodium gigantospermum* Aellen
Isoetes lacustris L.; E	**Cypripedium calceolus* L.†
Juncus filiformis L.; E	**Dryopteris goldiana* (Hooker) A. Gray
**Liatris scariosa* (L.) Willd.; SC	**Gentianopsis crinita* (Froel.) Ma
**Lygodium palmatum* (Bernh.) Sw.; SC	**Habenaria hookeri* Torr.
**Myriophyllum alterniflorum*; Alph. de Candolle; T	**Habenaria viridis* (L.) R. Br.
**Myriophyllum verticillatum* L.; E	**Lupinus perennis* L.
**Ophioglossum vulgatum* (Blake) Farw.; T	*Malaxis unifolia* Michx.
**Panax quinquefolius* L.; SC	**Polygonum tenue* Michx.

Table 4. Continued.

State-listed Species	Watch List Species
**Sisyrinchium mucronatum* Michx.; T	*Scirpus polyphyllus* Vahl
Sparganium minimum (Hartman) Fries; E	*Scirpus torreyi* Olney
**Stachys palustris* L.; H	**Selaginella rupestris* (L.) Spring
	**Silene caroliniana* Walter
	**Smilacina trifolia* (L.) Desf.
	**Sparganium angustifolium* Michx.
	**Stellaria borealis* Bigelow
Extirpated state-listed species = 19/170 = 11.2% of total extirpated species and 14/147 = 9.5% of documented extirpated species	Extirpated watch list species = 23/170 = 13.5% of total extirpated species and 18/147 = 12.2% of documented extirpated species

Species losses reported in several other comparative studies of vascular floras ranged from 3% to 46% (Table 6). Several variables might affect the magnitude of these losses, including the time elapsed between first and last censuses, the amount of change in the study area, the size of the study area, and the thoroughness of the surveys. Three studies from the United Kingdom (Sheffield, Glasgow, and Middlesex, including London), show relatively modest losses of 12% in ~100 yr., 11% in ~180 yr. and 10% in 100 yr., respectively. These areas would have been exposed to a long history of human disturbance before the initial censuses, perhaps eliminating some of the most sensitive species before the first survey. The low losses from Chester County, Pennsylvania may be due to the large size of this study area (1974 km^2). The high losses on Staten Island (46%) undoubtedly reflect the extensive landscape changes accompanying the immense

Table 5. Percentage of Worcester occupied by forest, wetland, and aquatic habitats: 1830–1982.

Year	Forest	Wetland	Aquatic
1830	22	5.0	1.2
1935	18	1.0	3.2
1951	28	0.9	3.5
1971	28	0.4	2.8
1982	18	0.7	1.6

Table 6. Rates of species loss among Orchidaceae and all species for different locations.

Orchid loss (%)	Overall loss (%)	Elapsed time (yr.)	Location	Source
53	18	~100	Worcester, Mass.	This study
19	6	~120	Concord, Mass.	Eaton (1974)
67	37	100	Middlesex Fells, Mass.	Drayton & Primack (1996)
33	19	100	Nantucket, Mass.	Sorrie & Dunwiddie (1996)
33	27	80	Three Mile Island, N.H.	Holland & Sorrie (1989)
16	3	150	Chester Co., Pa.	Overlease (1986, 1987)
75	19	50	Wisconsin; upland forest	Wiegmann (pers. comm.)
75	46	100	Staten Island, N.Y.	Buegler & Parisio (1982)
33	11	~180	Glasgow, Scotland	Dickson et al. (2000)
38	10	100	Middlesex, England	Kent (1975)
35	12	~100	Sheffield, England	Shaw (1988)
33	21	110	Auckland, New Zealand	Duncan (pers. comm.)
88	26	~110	Singapore	Turner et al. (1994)

growth in the island's human population. Middlesex Fells and Three Mile Island also have relatively high losses. A contributing factor is certainly the small size of both areas (400 ha and 17 ha, respectively). Beyond this, Middlesex Fells has been subject to intensive recreational use, reduced wood cutting and grazing, and increased isolation from adjacent natural habitats. Habitat losses on Three Mile Island appear to have been much less extensive, and native species losses there may simply reflect the vagaries of small populations on a small island. Losses in Worcester are in the middle of those reported in the cited studies. Compared to the other areas in Table 6, Worcester is intermediate in size (9740 ha). Much of it has been exposed to extensive land use changes, but extensive areas remain in relatively natural habitat.

Losses by habitat. Species losses were 10–25% in most habitats, mirroring the overall rate of species loss. However, a few habitats have more or less frequent extinctions.

The high losses from aquatic habitats could have several explanations. They could be an artifact either of the greater difficulty of sampling aquatic habitats, or of the fact that one major body of water (Lake Quinsigamond) straddles the Worcester/Shrewsbury town line. G. E. Stone, who collected extensively from this lake in the late 1800s, frequently did not specify in which town a collection was made. I included his records in the Worcester flora, reflecting the fact that about a third (several kilometers) of the lake's shoreline is in Worcester, and that my cursory observations of the Shrewsbury side yielded neither species nor habitats different from those on the Worcester side. Nevertheless, it is possible that a careful examination of the Shrewsbury side would turn up some of the species listed here as extirpated.

The losses of aquatic species have occurred in habitats that have varied both in quantity and quality. There were apparently only three substantial natural bodies of water in Worcester: Lake Quinsigamond, Indian Lake (formerly North Pond), and Bell Pond (formerly Bladder Pond). Undoubtedly there were also many beaver ponds, but these would have been eliminated along with their builders before the earliest plant collections reported herein. The many additional ponds that increased the extent of water in the City from 1.2% in 1830 to 3.5% by 1951 were created by damming of flowing waters. A dam also substantially enlarged the size of Indian Lake, from an original 12–16 ha to its present 89 ha. However, sedimentation, intentional filling, breaching of dams, and the trapping of streams in underground pipes have reduced surface waters by more than half from their 1951 peak. These reductions have undoubtedly had some effect on the flora. One example is *Potamogeton obtusifolius* Mert. & W. D. J. Koch, several specimens of which were collected from Beaver Brook at Chandler Street, a stream that is now underground.

While changes in the extent of surface water have undoubtedly affected the native flora, it seems likely that changes in water quality have had greater effects. Dam construction converts flowing waters to standing water. Other major alterations include sedimentation, chemical pollution, thermal pollution, use of aquatic herbicides, the conversion of relatively oligotrophic waters to more eutrophic waters, and the practice of draining water bodies (such as Indian Lake and Cook Pond) for weed control. The introduction of non-native species, such as *Myriophyllum hetero-*

phyllum Michx., *M. spicatum* L., and *Potamogeton crispus* L., may also have taken their toll. In another comparative study, Kent (1975) reported high rates of loss among aquatic, bog, and marsh species in the vicinity of London, England. He attributed this loss to draining and filling as well as to a general lowering of the water table. Extensive losses of aquatic and wetland species were also reported from Glasgow (Dickson et al. 2000).

The strongest and most consistent pattern in the habitat data is the loss of bog species, with losses amounting to at least a third of the original species in this habitat. This likely reflects the loss of a habitat that was relatively uncommon in the City to begin with. Several collections of now-extinct bog species from the late 1800s refer to "Floating Island" in Indian Lake. These species include *Chamaedaphne calyculata* (L.) Moench, *Larix laricina, Ledum groenlandicum, Sarracenia purpurea* L., and *Smilacina trifolia,* all now extirpated. It seems likely that this flora was erased when Indian Lake was dammed, increasing the water level. Another bog species (*Juncus filiformis* L.) was reported by Jackson (1927) from a "bog recently filled in" in South Worcester. While the lack of a specimen prevents us from confirming this species' identity, the comment indicates another threat to small bogs. Peat extraction was yet another threat to bog species, and was practiced in at least two areas, Broad Meadow Brook and Peat Meadow, in the 1800s (Anonymous 1879). No bogs remain in the City, though a few acidic swamps supporting *Solidago uliginosa* Nutt., *Drosera* spp., *Bartonia virginica* (L.) Britton, Sterns & Poggenb. and sphagnum occur. Compounding the probably limited original extent of bog habitat is the specialized nature of many bog species, apparently precluding their survival in other habitats. Further, if the original bogs were widely scattered, recolonization of locally extinct species would be difficult, even if habitat alterations were only temporary. In contrast with the results reported here, Dickson et al. (2000) were unable to confirm the extinction of even a single species of raised bogs in the vicinity of Glasgow. Unlike the presumed situation in Worcester, however, Glasgow bogs were relatively widespread. Despite extensive alteration, sufficient areas remain to retain the original flora. Dickson et al. do, however, report extensive losses among species of fens.

Given the substantial reductions in the area of wetland habitats in the past century, it is surprising that losses in all wetland categories are not higher. In fact, bogs are the only wetland habitat with above-average losses. All others are at or slightly below overall losses, and losses from swamps, based on the habitat designations of Magee and Ahles (1999), are significantly below overall losses. Several factors may have been operating here, and present information is inadequate to distinguish among them. One possibility is that wetland species, with the exception of bog species, are relatively unspecialized and can persist in a wide range of wet habitats. A related possibility is that wetland habitats are more dynamic than upland habitats as a result of the vagaries of weather and the activities of beavers, and wetland species have evolved resilient life histories to deal with these changes. Perhaps too, a wetland area that was not actually eliminated received less human influence than many upland habitats. For example, a swamp might be harvested for timber, but it could not be plowed, as an upland habitat might. There also may have been an increase in the extent of forested wetlands at the expense of wet meadows as the impact of beavers and fire were reduced. Finally, water may have served as an agent for the movement of plant propagules, thereby minimizing any deleterious influences of habitat fragmentation.

Among upland habitats, two show some evidence of excess species loss: coniferous and calcareous terrestrial. Both of these habitats are likely to have been much less common in the City than the predominant oak forests. The bedrock of southern New England, which generated the till that serves as parent material of the City's soils, is predominantly acidic. The limited extent of less acid soils is emphasized by the infrequency of calciphiles [as designated in the reference floras; e.g., *Adiantum pedatum* L., *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb., *Carex flava* L., *Cerastium arvense* L., *Eupatorium maculatum* L., *Matteuccia struthiopteris* (L.) Tod., *Osmorhiza longistylis* (Torr.) Alph. de Candolle, *Selaginella apoda* (L.) Spring, and *Sparganium eurycarpum* Engelm.].

Several coniferous habitats may have originally occurred in the City, though they were probably uncommon. Cedar (*Chamaecyparis thyoides*) was present, but probably infrequent, as is the case elsewhere in southern Worcester County. Uplands dominated by *Pinus strobus* L. and *Tsuga canadensis* (L.) Carrièrre may have been limited if the Indians regularly burned the landscape, as seems to have been true in other southern New England locales

(Bromley 1935; Day 1953). Today, cedar is absent, hemlock is infrequent and rarely dominant, and pine, though widely distributed, is dominant at only a few sites. The ten most common tree species in the City are all deciduous (Bertin, unpublished). The lack of conifer-dominated habitats may account for the absence of species such as *Goodyera tesselata.* However, most of the losses noted for the coniferous category are of species also found in non-coniferous habitats [e.g., *Smilacina trifolia, Cypripedium calceolus, Pogonia ophioglossoides* (L.) Ker Gawl., *Arctostaphylos uva-ursi*], so the high losses for coniferous habitats may be coincidental.

The past century has seen a reduction in the extent of grassland habitats such as pastures and meadows, which have undergone succession or been lost to development. For example, a reduction in hay fields can be seen by comparing aerial photographs from the 1950s with those taken more recently. A reduction in such habitats is sometimes invoked to explain the reduction or loss of certain species from our flora, such as *Castilleja coccinea, Ophioglossum vulgatum* L., and *Gentiana linearis* Froel. This trend was not obvious in Worcester, however. Species losses from grassland habitats were lower than overall losses based on habitat classifications in two sources and higher in one, but not significantly different in any case. While the extent of pastures and meadows has certainly declined, many of the denizens of such habitats seem to have persisted in other open habitats, such as lawns, roadsides, and power line clearings, and the widespread availability of such modified habitats has perhaps prevented higher extinction rates in grassland species.

Some workers believe that the incidence of fires in recent decades has declined substantially from their incidence in previous centuries (Whitney 1994). Frequent fires probably maintained certain habitat types in greater frequency than at present. For example, fires were likely to have been especially frequent in dry forests and would have maintained open, savanna-like conditions. Certain wetland habitats might also have been subjected to burning, which would probably have tended to increase the extent of marshes relative to that of shrub swamps and swamps. This study provides no evidence that species associated with fires or fire-maintained habitats have been disproportionately lost. Fires or burns are mentioned only in reference to four native species in any of the three sources, and only one of these, *Epilobium an-*

gustifolium L., appears to have been lost from the City's flora. Occasional fires set by vandals may have helped retain fire-maintained oak savanna in several parts of the City (Rawinski, Massachusetts Audubon Society, pers. comm.). Species of dry open woodlands had low rates of loss according to two classifications and high losses according to the third, but none of these differences was significant. Species from wet herbaceous habitats were lost at rates less than or equal to the rates for vegetated wetlands (a category that includes wetlands dominated by woody plants as well as those dominated by herbaceous plants).

Taxonomic pattern of losses. Of the taxonomic patterns of species loss reported here, some appear to be consistent with patterns of loss elsewhere, whereas others are more idiosyncratic. The most consistent pattern is for the Orchidaceae, discussed below. High losses among the Potamogetonaceae are consistent with results from the London area (Kent 1975) and from a 17 ha island in Lake Winnipesaukee, New Hampshire (Holland and Sorrie 1989), but not with results from Glasgow (Dickson et al. 2000) or Sheffield (Shaw 1988). High losses among the Lentibulariaceae were also noted by Dickson et al. (2000) for Glasgow and for two German floras. High losses in the Menyanthaceae and Haloragaceae in the Worcester flora are likely to be related to the aquatic or bog habitats of many of these species and do not necessarily mimic those reported in other studies in the northeastern United States. In examining species losses from a conservation area near Boston, Massachusetts, for example, Drayton and Primack (1996) reported extensive losses in the Lobeliaceae, Scrophulariaceae, Orchidaceae, and Primulaceae. Working on a 17 ha island in Lake Winnipesaukee, New Hampshire, Holland and Sorrie (1989) recorded the highest losses of native species in the Potamogetonaceae, Orchidaceae, Violaceae, Gentianaceae, and Rubiaceae. Most of these families differ from those experiencing the greatest losses in Worcester.

One family showing high losses both in Worcester and elsewhere is the Orchidaceae. About half of the original Worcester orchids have been extirpated, near the middle of the range reported for other sites (Table 6; Lamont et al. 1988). All 13 of the studies in Table 6 show orchid losses greater than overall species losses. The probability that this pattern would occur by chance alone is $0.5^{13} = 0.0001$. The sensitivity of orchids to local extinction in a wide variety of habitats and geographic areas suggests that they may be a good indicator of habitat "health" (Turner et al. 1994).

Several factors could contribute to the disproportionate loss of orchids. One is the rarity of many orchid species even in relatively undisturbed habitat (Hodgson 1986). Other things being equal, rare species are more likely to go extinct than common ones (Primack 1993). Orchids also have extremely small seeds lacking in endosperm and are dependent on external carbohydrate sources, usually provided by mycorrhizal fungi, for establishment and growth (Baskin and Baskin 1998). These traits may reduce their ability to recover rapidly from population decreases, and also expose them to the risk of factors that influence habitat suitability for their associated fungi. Their capacity for vegetative spread seems to be limited. Additionally, several species occur in bogs, and species in this habitat were especially prone to extinction in Worcester and perhaps elsewhere as well (Overlease 1987). Some orchid species have specialized pollination mechanisms that either require a specific pollinator or depend on pollination by deceit. These factors put orchids at risk from any factors that reduce pollinator numbers and may reduce the rate at which these plants can increase from population lows. A further threat to orchids is browsing by white-tailed deer (*Odocoileus virginianus*). A review of rare plants threatened by deer browsing included 21 orchids in a total of 98 species, a much higher proportion than that of orchid species in the overall flora (Miller et al. 1992). The authors were unsure, however, whether the high frequency of orchids reflected feeding preferences of deer or a bias in recording data. It is uncertain whether deer populations in Worcester have been sufficiently high to have had a major influence on vegetation. A final threat is collection by botanists or gardeners. Collecting by these individuals as well as for the horticultural trade may have contributed to high orchid losses in Singapore (Turner et al. 1994).

Conclusions. Apparent local extinctions of native vascular plant species from Worcester, Massachusetts have been considerable, amounting to approximately one in five species over the past century. The major causes have undoubtedly been habitat alterations resulting from human activities. These alterations have had their greatest effects in relatively few habitats, especially bogs and aquatic habitats. Certain plant families have been hit particularly hard, especially the Orchidaceae and a number of aquatic families. While there may be important differences in patterns of loss in urban and rural areas, the patterns described for Worcester are to some degree representative of statewide patterns. This is illustrated by the disproportionate representation of state-listed species among species that have gone extinct locally.

Losses of native species will continue in Worcester, accompanying the continuing alteration of habitats. Over time, the most conspicuous habitat alterations should decline as less undeveloped land remains for human modification. Undeveloped land will persist in the form of land that is protected or that is too wet or steep for development. However, species losses are likely to continue, reflecting in part the time lag between habitat reduction and local extinctions (Primack 1993; Turner et al. 1994). Drayton and Primack (1996) recorded the loss of over a third of native species during a 100 yr. period in a preserve near Boston. These losses were thought to have been caused by relatively subtle land use changes combined with isolation of the preserve from surrounding sources of propagules. An additional factor that may contribute to future species losses is global climatic change, particularly in areas with highly fragmented landscapes, which make colonization and recolonization difficult. While considerable tracts of land have been protected from development in Worcester over the last two decades, inevitable successional changes, more frequent passive recreational use, further fragmentation and isolation, impacts of non-native species, and climatic changes seem likely to cause substantial further species losses in the next century.

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APPENDIX

ADDITIONS AND CHANGES TO THE LIST OF NATIVE SPECIES IN BERTIN (2000).

Taxonomy follows Gleason and Cronquist (1991). *denotes species new to Bertin (2000); other species are those not previously documented with specimens. Specimen locations: WNHS (Worcester Natural History Society), NEBC (New England Botanical Club), MASS (University of Massachusetts).

FERNS AND FERN ALLIES

ASPLENIACEAE

*****_Dryopteris clintoniana_ (D. C. Eaton) Dowell – WNHS no date
*_Dryopteris goldiana_ (Hook.) A. Gray – NEBC 1878

ISOETACEAE

Isoetes echinospora Durieu – WNHS 1890

LYCOPODIACEAE

*_Lycopodium inundatum_ L. – WNHS 1890

OPHIOGLOSSACEAE

*_Botrychium oneidense_ (Gilbert) House – WNHS 1916

POLYPODIACEAE

Polypodium virginianum L. – WNHS no date

GYMNOSPERMS

CUPRESSACEAE

*_Chamaecyparis thyoides_ (L.) Britton, Sterns & Poggenb. – WNHS 1890

PINACEAE

*_Larix laricina_ (DuRoi) K. Koch – WNHS 1890

TAXACEAE

Taxus canadensis Marsh. – WNHS 1890

DICOTYLEDONS

ANACARDIACEAE

Rhus typhina L. – WNHS 1885

ASCLEPIADACEAE

**Asclepias tuberosa* L. – WNHS 1890, also observed growing in the City in 2001

ASTERACEAE

**Cirsium muticum* Michx. – WNHS 1914
**Eupatorium pilosum* Walter – WNHS 1894
**Liatris scariosa* (L.) Willd. – WNHS no date
**Vernonia noveboracensis* (L.) Michx. – WNHS 1890

BRASSICACEAE

**Cardamine rhomboidea* (Pers.) Alph. de Candolle – MASS no date

CABOMBACEAE

Brasenia schreberi J. F. Gmelin – WNHS 1890

CARYOPHYLLACEAE

**Stellaria borealis* Bigelow – WNHS 1929

CORNACEAE

Cornus rugosa Lam. – WNHS 1912

ERICACEAE

**Arctostaphylos uva-ursi* (L.) Spreng. – WNHS no date
**Kalmia polifolia* Wangenh. – WNHS no date
**Ledum groenlandicum* Oeder – WNHS no date

FABACEAE

**Desmodium rigidum* (Ell.) Alph. de Candolle – WNHS 1890
**Lespedeza virginica* (L.) Britton – WNHS 1919
**Lupinus perennis* L. – WNHS 1890
**Tephrosia virginiana* (L.) Pers. – WNHS 1890

LAMIACEAE

Stachys palustris L. – WNHS 1927 [the native var. *pilosa* (Nutt.) Fernald]
Teucrium canadense L. – WNHS 1934

LYTHRACEAE

Decodon verticillatus (L.) Ell. – WNHS 1890

NYMPHAEACEAE

Nymphaea odorata Aiton – WNHS 1886

ONAGRACEAE

**Circaea alpina* L. – WNHS 1890
Oenothera parviflora L. – WNHS 1938

POLYGALACEAE

**Polygala polygama* Walter – WNHS 1877

PRIMULACEAE

**Lysimachia hybrida* Michx. – WNHS 1899

PYROLACEAE

**Pyrola secunda* L. – WNHS 1890

ROSACEAE

**Fragaria vesca* L. – WNHS 1885
Potentilla arguta Pursh – WNHS 1918
**Sanguisorba canadensis* L. – WNHS 1890

RUBIACEAE

**Galium trifidum* L. – WNHS 1916

VIOLACEAE

**Viola primulifolia* L. – WNHS 1919

MONOCOTYLEDONS

ARACEAE

Calla palustris L. – WNHS 1878

CYPERACEAE

Carex cristatella Britton – misidentification, species deleted
**Cyperus dentatus* Torr. – WNHS 1918
Eleocharis robbinsii Oakes – misidentification, species deleted
**Eriophorum gracile* W. D. J. Koch – WNHS 1878
**Eriophorum virginicum* L. – WNHS 1891
**Rhynchospora alba* (L.) Vahl – WNHS 1890
Scirpus subterminalis Torr. – WNHS 1890

IRIDACEAE

**Sisyrinchium mucronatum* Michx. – WNHS 1938

JUNCACEAE

**Luzula acuminata* Raf. – WNHS 1878

LEMNACEAE

Spirodela polyrrhiza (L.) Schleid. – WNHS 1890

LILIACEAE

Aletris farinosa L. – WNHS 1890
Smilacina trifolia (L.) Desf. – MASS 1888
Streptopus roseus Michx. – WNHS 1888

ORCHIDACEAE

Cypripedium calceolus L. – WNHS 1880 (both large- and small-flowered varieties)
Goodyera pubescens (Willd.) R. Br. – WNHS 1876
Goodyera tesselata Lodd. – WNHS no date
Habenaria hookeri Torr. – WNHS 1898
Habenaria viridis (L.) R. Br. – WNHS 1912
Spiranthes lacera (Raf.) Raf. – WNHS 1885

POACEAE

Muhlenbergia uniflora (Muhl.) Fernald – WNHS 1890
Poa alsodes A. Gray – WNHS 1878

POTAMOGETONACEAE

Potamogeton foliosus Raf. – misidentification, species deleted

SPARGANIACEAE

Sparganium angustifolium Michx. – MASS 1890